Exploring Adaptive Functions of Geophagy Across Non-human Primates: New Evidence for Sexual Selection

An Honors Thesis (HONR 499)

by

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Abstract

Evolutionary theory predicts that non-immunological defenses against pathogens and toxins evolved as counter-measures to protect non-human primates during sensitive periods of development. The current study focuses on one type of non-immunological defense, geophagy, the consumption of soil. According to life history theory, pregnant females and juvenile non-human primates might be at heightened risk for the effects of specific infections and toxins due to immunological constraints. This study therefore predicted that geophagy would be observed more in pregnant and juvenile non-human primates. Data were collected by scanning databases: Agricola, Google Scholar, Web of Science, PubMed, and JSTOR. The search was initiated by searching for the keyword "geophagy" and scanning for entries related directly to that defense. I coded for age, sex, and reported function of geophagy. Findings suggest that the primary purpose for geophagy is detoxification and digestion. The secondary purpose being nutrition, and the third reported purpose being sexual selection. Contrary to the hypothesis and current findings in humans, adult males were reported to have similar observations of geophagy with adult females. However, the sex difference may be biased given the difficult nature of determining sex and age through scan sampling. My findings provide support for mainstream hypotheses of geophagy, with evidence towards both the supplementation and protection hypotheses. A newly reported function of geophagy points to sexual selection where researchers suggest that if adult males are consuming more soil, sexual selection might play a role, such that male-male competition may lead injured adult males to engage in geophagy as a method to boost iron levels or ward off parasitic infections from wounds. Alternatively, adult males could be using geophagy to signal good health; thus increasing the potential for mates. Future research should consider this understudied role of geophagy and other non-immunological defenses.

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Dr. Caity Leonardson-Placek was critical in the formation and execution of this project. Her patience in this long process and guidance is the reason I saw this thesis to completion. I would also like to thank the anthropology department Troyer Grant and Honors College travel grant for allowing me to present my findings at the American Association of Physical Anthropology.

Lastly, thank you to Em and Alex for sending encouragement and understandings when often times I stayed in the library for late nights.

Process Analysis Statement

If the fable of the tortoise and the hare taught me anything, it is that slow and steady can win the race. Is that okay if the race is university or a race to complete your thesis? If I were a character in this fable, I would undoubtedly be the tortoise wherein my five year journey has been a slow growth into my field of interest with primatology. This slow thesis race has now reached a little over a year mark; in fact, it was my twenty-second birthday when I finally met with my adviser to discuss the direction of my thesis and drink a celebratory iced chai tea latte. And here I am, a few months past my twenty-third birthday and I am now wrapping up this whole research process. It feels good to win this race.

During this long process, I have had doubts about marketability in primate research, doubts about my abilities in research, days of intense procrastination, and days where I sat in front of the computer for hours and wrote away. The whole thesis topic was born in doubt, in fact. I have, and occasionally continue, to struggle in an uncertainty in career paths. When settling with a topic I contemplated the job opportunities, unpaid research, and the necessity of being tied to a university; these all frightened me. Clearly, though, my passions for monkeys won out this long debate. After doubting the possibility of writing about something I feared job security in, I doubted my research abilities. Quite frankly, I did not feel adequately prepared to conduct a thorough literature review nor to write a rigorous report for the data findings. This doubt manifested in a few ways. First, I would procrastinate. As we are all well aware, this procrastination would exponentially increase my anxiety centered on being a poor researcher. These were the bad day- days in which I was stuck in a cycle of self-doubt and procrastination. However, these days were offset by the late nights, sipping caffeine, and feverishly typing away paragraphs. These nights, oddly, would get me thinking about the excitement of graduate school. I would envision more late nights and primate research but with a Dr. getting attached to my name.

As most do, my thesis started with the literature review. Even as I type this, I keep wishing that I had access to more article- to expand my literature review to larger datasets. Certainly this is a universal feeling- the learning process never truly feels over. After this literature review, I would semi-routinely meet with my adviser and learn how to code. It was my first time and, again, I had doubts about how I was doing. However, coding articles and creating spreadsheets ended up being one of the most enjoyable parts of this process. Before this I had thought of myself as more hands-on in research, but I may consider positions where I can conduct more literature reviews or areas where I can code data.

My next task was writing, and let me tell you, this probably took the longest. But upon reflection, this had to be the easiest part. I had all the information and data, I just had to concentrate for long enough to formulate it all. However, as I mentioned, on those good days I would be able to write long sections and had it nearly ready in less than a month. The revising process was not too bad, either. Although, I do regret parts of my writing style. When I’m in the moment, I do not cite things right away; instead, it takes me hours of sifting through my literature to make proper citations. It’s not a fun time.

Even through most of these self-imposed obstacles, it was fulfilling to see it to completion. There were nights I thought I would never finish, but here I am nearly 6,000 words later. It is hard to pinpoint my emotions because even through my relief, I feel sad. I think I viewed this process as the last thing before graduation. So with this thesis finished, I am finished. In less than five days I will finish this five year path.

Although I cannot say where my career in primatology will go, and in what research directions, but I am thankful for this opportunity to express these parts of my interest. I feel lucky that I was able to spend a full year reading and writing about something that made me happier. Even though sometimes it was a chore, it was one that I would come out in a better mood. When things felt overwhelming in other classes, or when I felt I was not making any progress, it was nice to be grounded be something I felt more of a connection to. The race is over, but I can take these skills and start a new one.

Introduction

Geophagy, the intentional ingestion of earth, is a form of pica. Pica is the craving and purposeful repeated consumption of nonfood items (Young et al., 2011). Soil, of course, is among these nonfood items, but so is ice, chalk, starch, baking soda, or laundry starch. The intentional ingestion of earth has been documented among all the chordate orders; which are: amphibians, birds, fish, mammals, and reptiles (Henry & Cring, 2013). Furthermore, geophagy in non-human primates is a widespread behavior; of these reported behaviors, early research found that 39 (21.1%) of primate species have been observed engaging in this behavior (Krishnamani & Mahaney, 2000). Krishnamani & Mahaney (2000) compiled an extensive list of the known primates who have been observed ingesting soils: as of 2000, 25% of great apes, 19.4% of prosimians, 15.6% of new world monkeys, and 26% of old world monkeys were observed engaging in geophagy. Since the nineteen years of this publication, more non-human primate species have been reported to ingest soil which would increase these rates. Furthermore, non-human primates do not ingest a singular soil type, they have been reported consuming soil from termite mounds, salty soils, leaf-cutting ant mounds, and soils for forest floors (Krishnamani & Mahaney, 2000).

There are six main hypotheses that explain why non-human primates engage in this behavior. Four of the hypotheses connect geophagy to alleviating gastrointestinal upsets and the other two relate to geophagy as a supplementation of necessary minerals. The hypotheses are as follows: geophagy is a means to (1) adsorb toxins and secondary metabolites; (2) adjust gut pH; (3) alleviate diarrhea; (4) combat against endoparasites; (5) provide greater nutrients for a poor diet; and (6) provide extra iron for those in high altitudes (Krishnamani & Mahaney, 2000). A seventh hypothesis of geophagy, briefly mentioned by Krishnamani & Mahaney (2000), is that geophagy is a non-adaptive behavior. According to this non-adaptive hypothesis, there is no physiological benefit to geophagy. Supporting evidence for this hypothesis includes the potential risks of consuming soil; such as: parasites, heavy metal or toxic chemical poisoning, bacteria and viruses, or vulnerability to predation (Pebsworth et al., 2018).

Hypotheses

There are four main tenets that relate to geophagy as a function to alleviate gastrointestinal upsets, which are mostly classified within the Protection Hypothesis. First, geophagy is predicted to shield non-human primates from the harmful toxins and parasites they might ingest. In terms of toxin avoidance, plants evolved secondary compounds (toxins) as a form of protection against herbivores (Speed et al., 2015); whereby some primate's gastrointestinal tract can digest these toxins others cannot. Individuals who lack the ability to process secondary compounds might consume clay to reinforce the intestinal wall. Young (2012) explains that the intestines are already protected by a layer of mucus; this is lined over the epithelial cells. Epithelial cells benefit from the layer of mucus because they are the cells that come into contact with ingested items. Food and waterborne pathogens can enter the bloodstream without the physical and chemical barrier. Clays can reinforce this mucosal layer which can be eroded by acidic food items. Secondly, clays function by adsorbing or binding to toxins and pathogens. The protection works before the toxins and pathogens reach the intestinal wall; thus being dispelled from the body without infecting the host. Non-human primates typically encounter toxins through their diet. The plant life consumed has evolved plant secondary compounds to protect itself from herbivores and pathogens (Glander, 1982); these toxins include: tannins, alkaloids, terpenes, and phenols. This hypothesis suggests that non-human primates have adapted to the consumption of plant secondary compounds through behavioral adaptations like geophagy, and would predict that geophagy might occur more often in locations with high volumes of plant secondary compounds.

Geophagy is also predicted to treat gastrointestinal upsets by altering the pH in the stomach. The ingestion of clay can adsorb organic molecules which act as an extra mucus protector thus functioning as an antacid. When consuming certain foods, non-human primates may produce volatile fatty acids which can decrease the stomach pH; which could result in a potentially fatal acidosis (Goltenboth, 1976). Geophagy may help to protect against these fatty acids by adsorbing the organic molecules in a buffering action. Just as kaolin has been suggested as an effective antidiarrheal agent, Daykin (1960) has also provided evidence that it is an effective antacid within veterinary practice. Another prediction of altering pH in the stomach is that the minerals in soil may work as a catalyst. In this they could increase the fermentation rates within non-human primates stomachs and reduce the production of fatty acids. Geophagy is also hypothesized to function as an antidiarrheal agent (Krishnamani & Mahaney, 2000). In support of this hypothesis, research shows that some soils contain kaolinite, an active ingredient of the pharmaceutical drug Kaopectate, which has the capacity to settle gastrointestinal upsets. The fourth tenant of the protection hypothesis suggests that the adsorptive properties of clay have another function in counteracting endoparasitic infections wherein the gastrointestinal upsets may be a result of heavy parasitic load to be treated by the ingestion of soil (Krishnamani & Mahaney, 2000).

The last two tenants follow the supplementation hypothesis, in that geophagy also provides micronutrient supplementation. The prediction associated with micronutrient deficiencies is that soil and clay may provide the consumer with the nutrients they are lacking; iron, zinc, and calcium are largely the nutrients studies predict individuals are seeking. Bailey et al., (2015) provides data on widespread global micronutrient deficiencies; in which pregnant women and children under five are at the highest risk of iron, iodine, folate, vitamin A, and zinc deficiencies (Bailey et al., 2015). As for larger mammals, George Davis (1968) shows that calcium along with phosphorus are the most commonly deficient elements (Davis, 1968).The soil would then be predicted to provide essential elements and minerals that were otherwise missing in the diet, geophagy would be an adaptive behavior because nutritional deficiencies can pose negative overall health trade-offs between growth, reproductive viability, and susceptibility to disease (Rode et al., 2003); thus, impacting critical life history traits for the individual. Lastly, geophagy has been proposed as a form of mineral supplementation for individuals in high altitudes. At high altitudes, iron depletion may support geophagy behavior for those who need to increase red blood cells. The ingested soils may provide the non-human primate elevated concentrations of necessary sodium, iron, and bromine (Krishnamani & Mahaney, 2000). This hypothesis has been examined mostly through geophagy in gorillas, but data could be collected on other animals ranging in similar elevations to understand the role of altitude and soil consumption.

A last hypothesis falls under a non-adaptive perspective. Within this consideration, geophagy is predicted to be a non-adaptive behavior in which no adaptive function is observable. Krishnamani & Mahaney, (2000) included this hypothesis by suggesting that there is no physiological benefit to eating earth. This is supported with evidence that ingesting soil has certain trade-offs and potential negative impacts like parasitic, bacterial, or viral infections, heavy metal or toxin ingestion, predation vulnerabilities, and hindering dietary iron uptake (Pebsworth et al., 2018).

It is critical to acknowledge that the adaptive function of geophagy may vary from species to species, and that even within species geophagy may serve various functions. As Davies & Baillie (1988) conclude, there is no reason why geophagy should have a single function when it is most likely that it serves many different functions at different times (Davis & Ballie, 1988).

Non-immunological Defense

Geophagy is broadly categorized as a non-immunological defense strategy. Non-immunological defenses are grounded in the notion that rapidly deploying immune system defenses are costly to animals, and a common link between classes of immune function is that their employment requires resources that hosts might otherwise need for some other function (Sheldon & Verhulst, 1996). Non-immunological defenses are mechanisms that are not traditionally considered a part of the biological immune system (Parker et al., 2011). Alternate defenses include behavioral avoidance; in which a non-human primate could be observed grooming, avoiding infected individuals, sleeping in clean nests, consuming soil, or consuming certain plants. These are but few of the known behavioral avoidances, and more longitudinal data in high parasite and toxic environments may yield more information. A recent trend in non-immunological defense research is self-medication. Rodriguez and Wrangham (1993) first defined it as zoopharmacognosy with the consideration towards plant-life only in self-medicative behavior; yet the discovery of other self- medicative behaviors has proved that term obsolete. Instead, self-medication is used by Huffman (2007) as behavioral strategies by which animals avoid or suppress disease transmission and treat/and or control its symptoms; thus enhancing health and reproductive fitness (Huffman, 2007). Currently, the function of geophagy is under debate. Some studies suggest it functions as a treatment whereas others predict it has a preventative function; thus its inclusion under self-medication is not yet fully agreed on.

Mounting an immune defense causes animals to invest less energy in reproduction and growth due to maintaining an energetically costly defense of which high metabolic requirements of immune cells and immune upregulation are required. Sheldon & Verhulst (1996) provide evidence that immune function is costly through observations that poor nutrition is often associated with disease; more so they provide evidence from researchers that have documented that the high energetic need and nutritional depletion of an immune response will interfere with the metabolic function needed to reproduce (Sheldon & Verhulst, 1996). Non-human primates, and other animals, are constrained by limitations in resource availability; therefore it is necessary for them to balance their energy in terms of immune responses and competing life history traits (Canale & Henry, 2010). Non-immunological defenses function as a way to balance the competing need for energy and health maintenance, they achieve this by reducing the likelihood an individual may become exposed to toxins or poisons; thus balancing the competing needs of maintaining immune function and maintaining health (Sheldon & Verhulst, 1996).

Another topic emerging in immunological research is this concept of ecological immunity; which is concerned with the evolution of the immune system. This research considers ecological processes; such as, population genetics, interaction with parasites, intraspecific constraints, and additional interactions through prey, microbiota, etc. It suggests that places with high diversity of ecological processes will result in more diversity in immunological mechanisms. Basically, different environmental conditions will allow for the evolution of diversity of immune defenses; more so, a main trend is to explain alternative defense variation by invoking trade-offs of immune defenses depending on ecological conditions (Schulenburg et al., 2009).

Life History Theory

Life history theory is a field of ontogeny concerned with the strategies an organism uses to allocate energy towards growth, maintenance, reproduction, raising offspring, and avoiding death (Bogin, 1999). The life history approach attempts to explain how life history traits are significant during an organism's lifetime, and how changes during a given time may impact fitness. Such life history traits are subject to trade-offs and constraints; therefore, natural selection cannot maximize fitness beyond certain constraints that are outside of the organism's control.

Ultimately, life history theory aims to understand adaptation. The allocation of energy and resources to one life history trait over another causes trade-offs; such as when growth in the juvenile stage is taking energy away from immune system maintenance. A core understanding in life history theory is that not all traits can have energy invested in them at all times; thus an individual must allocate between growth, reproduction, and avoidance of death. Closely related to this idea of trade-offs is the concept of constraints, which can be understood as a natural limit, like death, on an individual's potential of fitness. During pregnancy, for example, energy is being invested into the growth of the fetus; therefore, there is an immunological trade-off in the ability to ward off toxins and parasites, which would typically be protected against by the immune system. Geophagy, then, is predicted to protect during these times of trade-offs between growth and immune function. As reported by Flaxman & Sherman (2000), pregnancy is a vulnerable life stage in which women experience more gastrointestinal distress, what they define as morning sickness, where they become partially immunosuppressed in an attempt to avoid a natural rejection of the developing fetal tissues. This vulnerability is a result of the maternal-fetal conflict in which the maintenance of the mother's health is compromised during the fetal growth period where both are in competition for nutrients (Scholl et al., 1994). Susceptibility for pathogens and toxins increases during life stages where rapid cell division occurs; these being, pregnancy or juvenile stages. Data published by Festa-Bianchet (1988) showed that lactating bighorn ewes had higher counts of ringworm in fecal collection than did non-lactating ewes (Sheldon & Verhulst, 1996). This evidence might suggest that allocating resources to reproduction comes as at a cost of resources available for immune defenses; thus pregnancy becomes a vulnerable life stage. Avoidance of toxins and pathogens would be more critical to this group more so than any other age or sex because of their trade-off between growth and immunocompetency

Predictions

I predict that due to an increase of vulnerability in juvenile and pregnancy stages, as a result of life history trade-offs, these target groups will exhibit more proactive non-immunological defenses in the form of geophagy against toxins and pathogens.

Methods

My hypothesis was tested by conducting a literature review. The following databases were included: Agricola, Google Scholar, Web of Science, PubMed, and JSTOR. The search was initiated by searching for the keyword "geophagy" and scanning for entries related directly to that defense. After coding articles, I utilized reference lists to identify more original data. To avoid translation errors on data, literature in other languages were not coded for due to a lack of proper translating capabilities. The date of published work was not considered so that I could be as comprehensive as possible; the earliest literature on non-human primate geophagy dates to

1978 (Oates, 1978) and the most recent literature dates to 2018 (Pebsworth et al., 2018). One goal of this study was to use originally published data so that I could reduce the chance of duplicated analysis of reported geophagy (Young et al., 2011). Data were categorized by creating a codebook that coded for taxa, geography, diet, sex, age-class, reproductive status, type of earth, and function of geophagy.

The criteria for including publications depended on whether they focused on: (1) non-human primates; (2) provided some sort of hypothesis for the function. Furthermore, all forms of geophagy were included; which encompassed earth materials that were consumed from various locations such as: mineral licks, clay, clay-water, soil, termitarium mounds, nests, or regolith.

Summary Statistics

Taxa

The literature review revealed twenty-one species of non-human primates that engaged in geophagy, with a repeat of four species in different reported instances: *Pan troglodytes, Pongo pygmaeus, Saguinus mystax, Macaca mulatta*. In two reports, the authors wrote "hybrid macaques" to signify a mixture of three different macaque species observed engaging in geophagy (Bolton et al., 1998; Burton et al., 1999).

The available reports only identified geophagy within the suborder haplorhini. Within parvorder, I identified 43% as platyrrhini (new world monkeys) and 57% as catarrhini (old world monkeys). The literature review revealed reports of geophagy in the following subfamies: Calitricinae, Atelinae, Pithecinae, Cercopithecidae, Colobinae, Ponginae, Gorillinae, and Hominidae. In another systematic literature review, it had been discovered that geophagy has yet to be observed in *Aotidae, Cheirogaleidae, Dauben-toniidae, Galagidae, Lorisidae, or Tarsiidae*, but it has been observed so far in one family of nocturnal non-human primates: *Lepilemuridae* (Pebsworth et al., 2018).

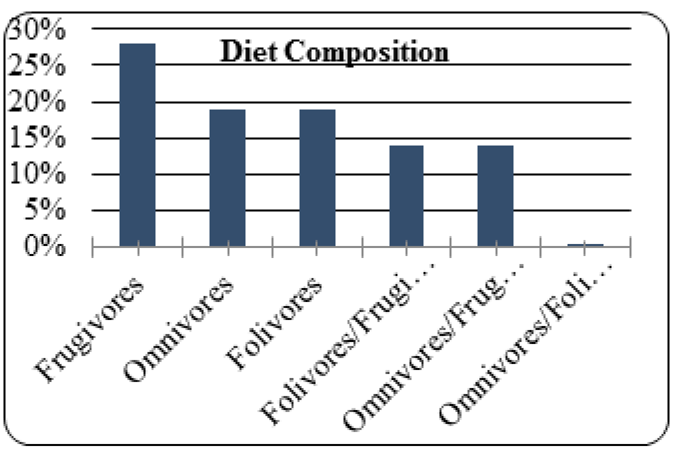
Geography

As for location, 38% of reported geophagy occurred in Asia, 38% occurred in the Neotropics, and 23% occurred in mainland Africa. Geophagy was observed in 13 countries: Ecuador, India, Brasil, Japan, Peru, Puerto Rico, Rwanda, South Africa, Uganda, Borneo, China, Columbia, and Malaysia.

Diet

In terms of diet composition, 28% of the non-human primates engaging in geophagy were frugivorous, 19% were omnivorous, 19% were folivorous, 14% were folivorous/frugivorous, 14% were omnivorous/frugivorous, and .4% were omnivorous/folivorous (Fig. 1).

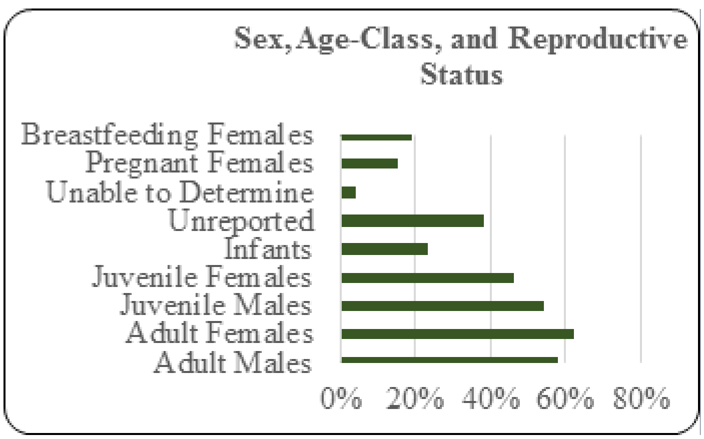
Figure 1. Diet composition of non-human primates engaging in geophagy



Sex, Age-Class, and Reproductive Status

Out of 26 studies, 15 reported on adult males (58%), 16 included adult females (62%), of which four of these included four pregnant females (15%) and five included breastfeeding females (19%). There were 14 studies that reported on juvenile males (54%) and 12 juvenile females (46%). One study was unable to determine the sex of the adults and juveniles (4%). Six studies had infants (23%). Ten of the 26 studies (38%) did not report age or sex of primates (Fig. 2).

Figure 2. Sex, age-class, and reproductive status of non-human primates engaging in geophagy



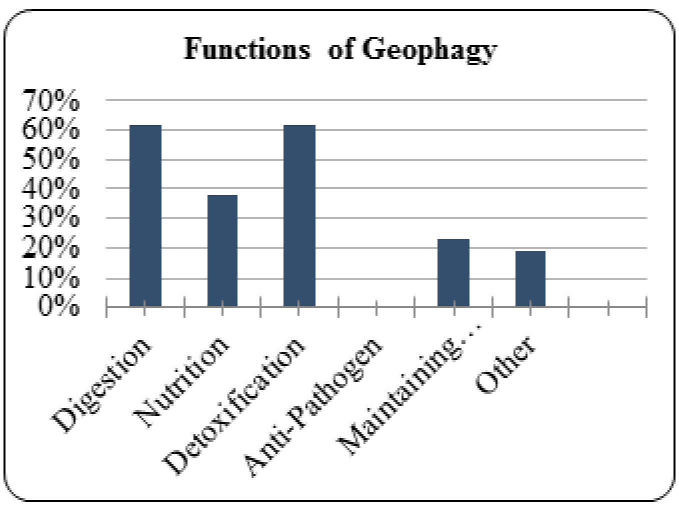
Type of Earth

Details regarding the types of substances consumed varied in specificity, with some being very general (e.g. “soil”) and others detailed (e.g. mineral soil high in Fe). As a result, substances were recoded into generalized categories. Twenty-six studies reported only one type of substance, and two reported two substances. Substances included: mineral licks (12%), soils (27%), mineral soils (.07%), insect mounds (31%), clay (23%), and regolith (.03%).

Function of Geophagy

Out of 26 studies, all reported at least one function of geophagy, with a maximum of three possible functions. The functions for geophagy included: detoxification (62%) and digestion (62%) both of which were reported 16 times as one of the cases of geophagy. Digestion was reported the most at 12 times (46%) for primary function followed by nutrition five times (19%), detoxification four times (15%), anti-pathogen two times (0.07%), and maintaining health one time (0.03%). In total, digestion and detoxification were suggested as the function 62%, nutrition 38%, anti-pathogen 0.07%, and maintaining health 23%. Other reported functions included: diet, environment, predation, taste, and sexual selection; these reported as 19% of the functions (Fig. 3).

Figure 3. Functions of Geophagy



Discussion: New Evidence for Sexual Selection

The purpose of this study was to codify the patterns and functions of geophagy; in which a systematic review of current literature would result in support for or against current hypotheses of its function. After extracting data from evidence, my findings from the systematic literature review revealed that geophagy is multifunctional and adaptive; thus, neither the protection nor supplementation hypotheses can fully explain the function of geophagy by itself. However, it did reveal that the main reasons for engaging in geophagy may be detoxification and digestion with new evidence for sexual selection.

Non-human Primate and Human Comparisons

When considering the role of geophagy, it is essential to consider how it functions in human populations. Researchers may be able to make conclusions on non-human primates due to the data that exists on the consumption of soil by humans. Moreso, examining the differences may allow us to better assess health risks associated with soil ingestion, assess any research bias in human research, and think about geophagy as a coevolutionary arms race with toxins and pathogens in the environment.

Diet

The diets of non-human primates are inherently related to their ecology and have an important function in the development of variation in dentition, digestive systems, body sizes, and microbiomes. Food habits of non-human primate species typically consist of a folivory, frugivory, insectivory, or a combination of these. Yet, seasonal fluctuation affecting the availability of preferred foods may influence variation of diet between and within groups; however, Hawes & Peres (2013) reported general trends of the primate diet in light of variation. According to the meta-analysis, the medium-sized primate diet is dominated by fruits, larger primates tend to eat more foliage as a function of the gastrointestinal tracts ability to tolerate secondary compounds, and smaller primates eat more insects. These smaller species require higher quality sources of nutrients and calories because of the high metabolic requirements of their body size.

My findings lends support for the protection hypothesis since both fruits and leaves are known to contain secondary plant compounds. They slightly differ from the meta-analysis of Pebsworth et al., (2018) who found roughly equal numbers of non-human primates that engage in geophagy with diet compositions of folivory and frugivory. My data is less equal at 28% for frugivory and 19% for folivory; however, this may be a result from my smaller sample size. Krishnamani & Mahaney, (2000) has similar findings in dietary strategies. They reported around 28.2% as folivorous and 20.5% as frugivorous and the rest belonged to a mixture of dietary strategies. In terms of human geophagy, data is difficult to correlate with dietary strategies since humans are typically omnivores and most research does not specify the dietary behavior of humans engaging in geophagy. However, Young et al., (2011) does provide data on clay material being used in food preparation as a means to neutralize toxins. In these dishes, the food eaten contained harmful substances and the clay worked to absorb these toxins.

Not yet discussed is the debate on whether geophagy functions as a supplementation of missing nutrients or geophagy being caused by nutritional deficiencies, such as iron. The main argument for the latter is that anemia may cause the craving of soil, and ingesting it will worsen the case. However, there are data that suggests anemia, even if causing geophagy, is an adaptation. Anemia can be a nutritional adaptation in a response to infections whereby limiting the body’s available iron will function to protect against bacteria which requires iron to reproduce (Denic & Agarwal, 2007). Thus geophagy, again, is seen to be multifunctional in that is may protect against bacteria that feeds on iron by causing anemia and by coating the mucosal layer thus physically protecting against toxins and poisons.

Location

If we are examining geophagy only as a functional defense against plant secondary compounds, we might assume that specific locations might have higher rates of it. Location would also be critical if we were assessing the parasite-burden and geophagy; whereby the tropics is high in parasite prevalence (Young et al., 2011). My data reported geophagy in 13 countries, and the associated biomes of these areas were typically tropical rainforests. Rainforests soils are poor in nutrients which may lend support for the supplementation hypothesis if the soils are in low quality of nutritional needs. In comparison with the meta-analysis of Pebsworth et al., (2018), I had more equal accounts of geophagy in Asia, Neotropics, and Africa, whereas they were surprised with less than expected results in the Neotropics and more than expected in Asia (Pebsworth et al., 2018). Again, this difference in conclusions may be a result of the smaller sample size. Krishnamani & Mahaney, (2000) reported more generally on geophagy in new world and old world primates, and concluded that the ecological data on non-human primate species are difficult to collect due to the difficult conditions in the tropics. It is not as difficult to gather geophagy data on humans, though. As a result, Young et al., (2011) were able to construct a map of reported cases of geophagy and the span of it is much larger. They include reports on every continent.

Sex and Age-Class

In the meta-analysis by Pebsworth et al., (2018), the frequency by sex and age-class differed from my findings. According to their results, geophagy occurred more often in females than males; yet, the researchers only documented variation in geophagy between males and females in 15 of the 287 accounts. In addition, they published that only one study distinguished ages of males which concluded that the frequency of geophagy occurred more in adult males over sub adult males (Pebsworth et al., 2018). In contrast, my results did not support such a higher frequency of geophagy in adult females; instead, adult male have similar rates. My data also differed from Pebsworth et al., (2018) in that I was able to codify for age-class for 96% of the published work. Krishnamani & Mahaney, (2000) meta-analysis of the adaptive significance of geophagy concluded that there was not enough data to show if there is significant difference in age and sex class in geophagy (Krishnamani & Mahaney, 2000). Taking into consideration my smaller sample size and the fact the Pebsworth et al., (2018) only reported on 15 out of 287 which included data on sex and age-class, Krishnamani & Mahaney, (2000) may be right in that it is difficult to assess significance from smaller pools of data. Again, this is a limitation. Researchers gathering data on geophagy may find it difficult to quickly assess the sex and age-class of primates engaging in acts that might not last long.

In human research, research has been biased towards researching geophagy among women and children, which may be why data is skewed towards higher rates of women engaging in it- particularly by those who are pregnant or have been pregnant. This may be a barrier to examining geophagy through new perspectives like sexual selection. Golden et al., (2012), although a study of human pica activity, reported similar conclusions in terms of sex. This article outlines an importance of population-based studies of pica that include males of all ages considering their data reported a high prevalence among men and an absence in the peak of geophagy during pregnancy. These results are counter to the research-bias that exists in pica research where studies in humans are mainly focused on women and children. They conclude that there is no significant difference between adult male and females that engage in pica activity; thus, this data should provide incentive to collect data on the behaviors across the sexes (Golden et al., 2012).

The study of geophagy varies across species; thus we may not observe the same functions between non-human primates and humans. For example, human consumption of soil has another function, or reason, that is not observed in non-human primates: the symbolic meaning behind it. As a medicine, soil can be prescribed as spiritual treatment to bring good luck; this treatment type accounted for 51.4% of medicines in a case-study in Madagascar (Golden et al., 2012). Young et al., (2011) also addresses the cultural aspects of geophagy not seen in non-human primates. They write that preconceived notions about geophagy have biased reporting, they found that geophagy was attributed to the "weaker sex" (Young et al., 2011). Culture will complicate the study of geophagy in humans, such that taboo around consuming non-food items may skew data. Placek & Hagen (2013) also demonstrates how culture may influence pica behavior through religious significance, healing, fertility, and childbearing (Placek & Hagen, 2013). More so, geophagy behavior can be encouraged in human populations when it is connected to religious identity. For example, small tablets of sacred earth are sold commercially, and are said to be blessed by the Roman Catholic Church (Hunter & de Kleine, 1984).

Another difference within human and non-human research in geophagy is the implications and reasoning for the studies. Pica is generally considered a public health interest due to its potentially negative and positive health outcomes; negative health consequences might include reducing bioavailability of nutrients, introducing toxic substances, or acting as a vector for parasitic infections. These are the same negative health consequence we might observe in non-human primates. Humans also share the potentially positive outcomes as non-human primates in that pica may provide protection against pathogens and toxins, quell gastrointestinal upsets, or provide beneficial nutrients. Pica is seen as a public health interest due to its prevalence among the most biological vulnerable populations; which are pregnant women and children (Golden et al., 2012).

Clearly, there is an advantage to studying geophagy in humans: verbal communication. Non-human primates cannot give us the reason why they engage in the act nor tell us if they are treating specific symptoms. For this reason, the human comparisons are critical to non-human studies so that researchers can base hypotheses and behavioral data on how it is observed, and explained, through human consumption. However, research in the human consumption of soil should be conducted in such a way that sociocultural and biomedical contexts of geophagy are taken into consideration due to the often deeply rooted nature of the behavior in various communities (Luoba et al., 2004).

Sexual Selection

An interesting finding that arose from the literature review was a consideration for a new function of geophagy: sexual selection. The authors suggested that during the mating season fighting amongst rival males, as well as females, might result in wounding; thus, geophagy could act as a potential to boost erythrocytes, or red blood cells, in the blood (Hsu et al. 2001). It may also function to protect against pathogens and toxins that might result from wounds. This may have important implications for mating. Nunn (2006) provided intriguing evidence that suggests that female mammals will avoid mating with males that are overtly parasitized; which suggests that the female mammals are exhibiting pathogen avoidant behavior. Pathogen avoidant behavior would increase fitness benefits for the females since parasites may be transmitted during mating; this is supported by evidence by Norris et al., (1994) who found that after manipulating brood size in great tits, males see a raise in increased parasitization whereas females do not (Sheldon & Verhulst, 1996). This may relate to the hypothesis that males who have greater fitness, possible due to higher testosterone and secondary sexual traits, are more likely to have a trade-off with immune function. In addition, males that are highly parasitized might not have the energy to devote to raising offspring; therefore, mating with these individuals would be risky for the survival and fitness of offspring. Health signaling is another interesting function that might be correlated to consuming soil after rivalry; the behavior might reflect positive health outcomes for detoxification, anti-pathogen, or maintaining health which would signal potential mates of overall good health. The treatment of parasites through geophagy could provide fitness benefits as that parasites may have negative costs on hosts, the energy used to maintain health and reproduce would be diminished because that energy is being used to mount an immune defense against the parasites. As I have mentioned, mounting an efficient immune response takes high amounts of energy and resources; thus, non-human primates that are maintaining this immunity are trading- off with other functions; such as reproduction. Consequently, relative fitness is lowered as they are not producing offspring. Another interesting possibility that future researchers should investigate is male non-human primate testosterone levels during rivalry and its relationship to geophagy. Studies provide that testosterone depresses that immune system; thus making males more susceptible to diseases, this is associated with the immunocompetence handicap hypothesis. Research is providing evidence that androgens can have immunosuppressive effects which is a trade-off to the development of sexual traits; more data on the relationship between the endocrine system and the immune system could provide even more insight on the trade-offs between sexual selection and immunity (Folstad & Karter, 1992). Data could be collected on this by measuring sexual ornament exaggeration and parasite-burden. This would provide support for either ornament exaggeration decreasing immunocompetence, and therefore being costly to put energy towards, or having no effect on it. Observing geophagy more in adult males, then, would make sense taking sexual selection, immunity, and parasites into consideration. It is shown that testosterone is also linked with a higher pathogen burden in non-humans. A possible explanation for this suggest that males might be exposed to higher parasite loads because they must use more energy while competing with rivals which may expose them to more parasites. If researchers studying geophagy keep these ideas of testosterone into consideration, they might be able to measure testosterone levels before and after consuming soil. In this research, the pathogen burden should be assessed. If the individual male are consuming soil, have high parasite-loads, and high testosterone levels this may lend support to this emerging link between geophagy as an adaptive function of sexual selection. This new evidence is surprising and it highlights an important function of geophagy that has been ignored in human literature.

Limitations

The limitations of this study are mostly related to conducting a literature review. You can never be as exhaustive as you wish; in this study, the amount of literature I wanted and what I ended up with did not match. Access to literature is also a limitation where there were some journal articles that were not accessible nor were they translatable; thus the sample size is small.

Conclusion

Overall, geophagy may end up being multifunctional for specific situations; whether that is for detoxification, digestion, or others. More in-depth data collection of it may allow scientists to make even more novel hypotheses on its functionality. Going forward, I might suggest that researchers include as much information; such as, sex, age-class, reproductive state, nutritional status, health, time of day, its duration, location, climate, and earth material data, so that it can be examined holistically. Non-human primates are increasingly facing anthropogenic and environmental challenges that are affecting dietary habits, and understanding geophagy may offer insight into conservation initiatives that focus on protecting natural food sources. We could also use our knowledge of geophagy to maintain the health of non-human primates within captive populations. Overall, researchers should consider this understudied behavioral adaptation for its implications in conservation and diet of non-human primates and its relevance for human populations that also engage in geophagy.

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